

Small mammal community composition in the Volcanoes National Park, Rwanda

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Abstract. Terrestrial small mammal community composition was examined in the Volcanoes National Park (VNP), Rwanda with respect to variation in habitat type and altitude. Trapping resulted in the capture of 220 individuals including eight species of rodents, three species of shrews and one mongoose. Of the species captured, *Praomys degraaffi* is vulnerable and *Sylvisorex vulcanorum* is near threatened (IUCN 2012). Six species (*Hylomyscus vulcanorum*, *Mus bufo*, *Praomys degraaffi*, *Sylvisorex vulcanorum*, *Lophuromys woosnami* and *Tachyoryctes ruandae*) are endemic to the Albertine Rift. Species richness and diversity varied significantly among the different habitat types as they increased with elevation up to the middle altitudes (2860–3255m) and then declined with increasing elevation. Altitude accounted for 20 % of the variation in species diversity. Species variation in habitats and altitude was related to environmental factors. Endemic species were found mainly in low and middle altitude habitats; thus these habitat types are important for conservation of small mammals at Volcanoes National Park.

Key words. Rodentia, Soricidae, Volcanoes National Park, endemism, diversity, elevational gradient, community structure.

INTRODUCTION

Baseline data are essential for biodiversity monitoring, especially during this era of anthropogenic and climatic change. However, the lack of accurate data on the status of free-ranging wildlife populations may limit the efficacy of monitoring programs. The African montane primary forests of the Albertine Rift are home to many endemic mammal species (Hutterer et al. 1987; Kerbis Peterhans et al. 1998; Kaleme et al. 2007). The Volcanoes National Park, gazetted as Parc National des Volcans in 1925 (hereafter VNP) is an afromontane forest rich in mammal species and endemism and is continuous with adjacent volcanoes in the Democratic Republic of Congo and Uganda. Many small mammals exhibit narrow habitat preferences and the distribution and abundance of small mammals may be indicators of ecosystem health (Golley et al. 1975). Habitats with low vegetation diversity house relatively few species (Kaleme et al. 2007), and altitudinal variation also influences small mammal diversity (Kerbis Peterhans et al. 1998).

The VNP is thought to support more than 25 small mammal species (Gyldenstolpe 1928; Hutterer et al. 1987). However, few studies on the ecology and community characteristics of small mammals (rodents and shrews) have been done in the VNP region (Gyldenstolpe 1928; Hutterer et al. 1987). While a considerable amount of work

has been carried out on the vegetation, birds and large mammals of VNP, including the critically endangered *Gorilla beringei beringei* Matschie, 1914 (Plumptre 1991; Fischer & Hinkel 1992; Robbins et al. 2001; Owionji et al. 2005), small mammals remain poorly documented. The only scientific publication on small mammals in the VNP was written over 80 years ago (Gyldenstolpe 1928) when 20 species were noted (data included in Table 1), but detailed small mammal diversity and distribution patterns were not determined. Since then, there has only been one unpublished study by Kajonjoli in 1993, rendered incomplete by 1990's Rwandan civil war and the unpublished report (data included in Table 1) on the Ugandan slope of Mgahinga Gorilla National Park (MGNP) by Kerbis Peterhans & Austin (1996).

Information on small mammal distribution and abundance across diverse habitats and along an elevational gradient in VNP will be useful to supplement additional scientific data for understanding structure and variation of small mammal communities. In this paper, we document small mammal community characteristics at VNP based on our recent collecting program, and specifically (1) compare small mammal abundance, diversity and distribution in eight habitats (Bamboo, *Hagenia* Woodland, Brush Ridge, Mixed Forest, Herbaceous, Sub Alpine, Alpine

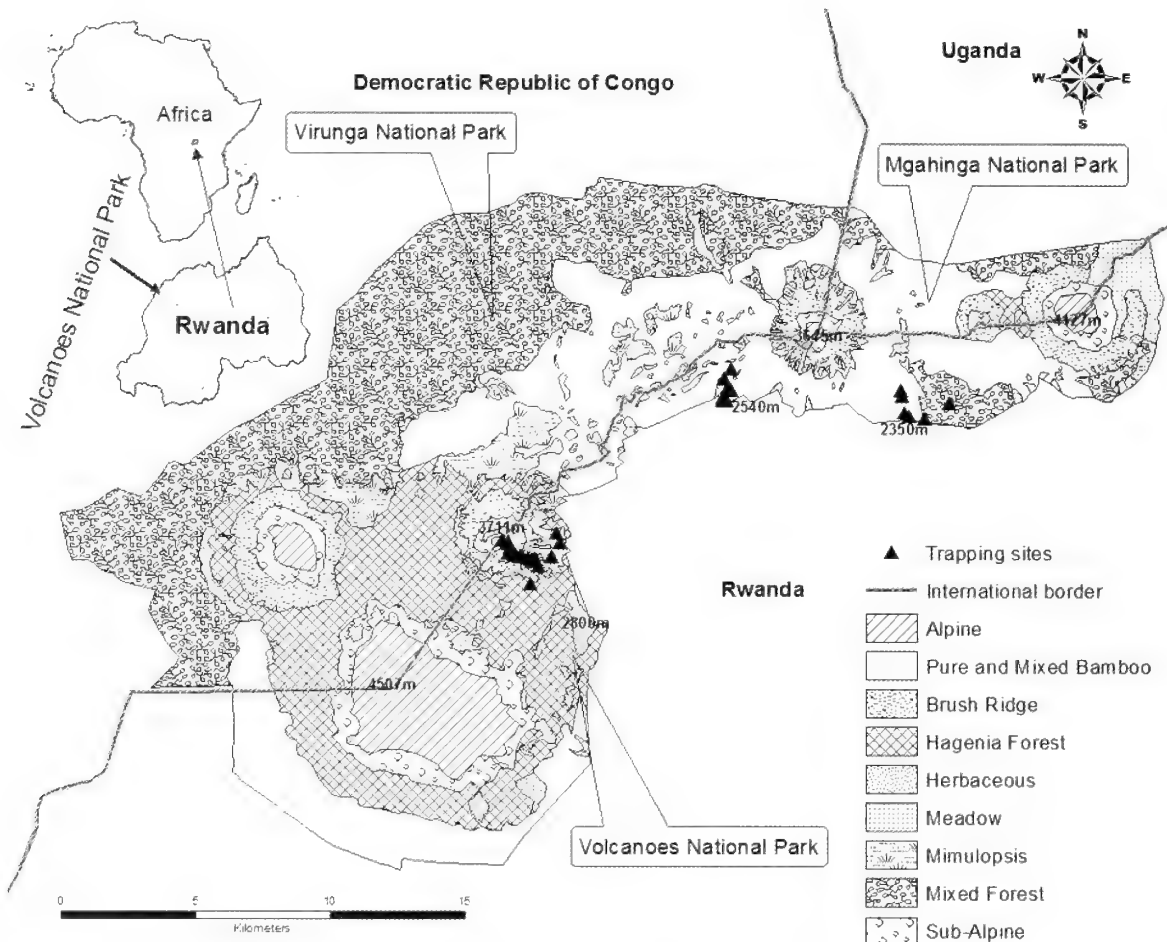


Fig. 1. A map of the Virunga massif illustrating the major vegetation zones and the locations of the trapping sites in the VNP.

zones, and Swamp); (2) assess levels of diversity in relation to altitude, environmental variables and habitat characteristics. (3) Finally, we provide data from two previous studies that contribute to assessing changes in Virunga small mammal diversity and abundance over the past.

MATERIAL AND METHODS

The study area

The Volcanoes National Park, Rwanda (between $1^{\circ}21'-1^{\circ}35'S$, $29^{\circ}22'-29^{\circ}44'E$) is a mountainous region, ranging in altitude from 2300 m to 4500 m (Weber 1987). It is located on the eastern edge of the Albertine Rift, which forms part of the watershed between the Nile and Congo River systems (Weber 1987). It lies in north-western Rwanda and borders its sister parks, the Virunga National Park (ViNP) in the Democratic Republic of the Congo (DRC) and Mgahinga National Park (MGNP) in Uganda. The Volcanoes National Park (VNP), ViNP and MGNP

(Fig. 1) form the Virunga volcanoes area (Virunga massif). This study was carried out at three sites in the Volcanoes National Park, Rwanda (Mts. Visoke or Bisoke, Sabyinyo or Sabinio and Gahinga) from October 2 to November 8, 2009. The selection of study sites was based on altitude and the major vegetation zones of VNP (Fig. 1). The major vegetation zones surveyed include: (1) Mixed Forest, (2) Bamboo, (3) *Hagenia* Woodland, (4) Herbaceous, (5) Brush Ridge, (6) Sub Alpine zone, and (7) Alpine (Plumptre 1991); swamps were categorized as an 8th zone.

For Table 1, we add data from two historical collections. The first reflects the efforts of the Swedish Zoological Expedition to the 'Birunga Volcanoes' from February to March, 1921 (Gyldenstolpe 1928). The second collection includes the species records from a more recent report (Kerbis Peterhans & Austin 1996) that gathered baseline data on terrestrial small mammal communities surrounding Kabiranyuma Swamp on the saddle between Muhavura and Mgahinga (2980 m) as well as land reclaimed for the park (2810 m) from evicted settlers, just on the Ugan-

Table 1. Small mammal species recorded in the Virunga massif then and now. Area codes: Burunga (B), Chahafi (Ch), Karisimbi (Ka), Kibati (Ki), Lulenga (L), Lake Mutanda (LM), Mgahinga (Mg), Muhavura (Mu), Mikeno (Mi), Ninagongo (Ni), Ngoma (Ng), Sabinio (Sa), Tamohanga (Ta), Tsitsilonga (Ts), Visoke (Vi). References (Ref.): (1) Gyldenstolpe (1928); (2) Kerbis Peterhans & Austin (1996); (3) this study.

Species	Elevations	Mtn (area)	Ref.
<i>Crocidura niobe</i> Thomas, 1906	2980	Mg-Mu	2
<i>Crocidura olivieri kivu</i> Osgood, 1910	up to 3300	B,Ki, Lu,Mi,Ta	1
	2810	Mg	2
	up to 3700	Vi	3
<i>Crocidura tarella</i> Dollman, 1915	2900	LM	1
		Vi	3
<i>Paracrocidura maxima</i> Heim de Balsac, 1959	2810	Mg	2
<i>Suncus megalura</i> (Jentink, 1888)	2810, 2980	Mg, Mg-Mu	2
<i>Sylvisorex lunaris ruandae</i> Lönnerberg & Gyldenstolpe, 1925	2600	Sa	1
	2810, 2980	Mg, Mg-Mu	2
<i>Sylvisorex vulcanorum</i> Hutterer & Verheyen, 1985	2810, 2980	Mg, Mg-Mu	2
	2980	Vi	3
<i>Myosorex babaulti</i> Heim de Balsac & Lamotte, 1956	2980	Mg-Mu	2
<i>Heterohyrax helgei</i> Lönnerberg & Gyldenstolpe, 1925	3500–4000	Mi, Sa	1
<i>Hystrix stegmanni</i> Muller, 1910		Mu,Sa	1
<i>Aethosciurus ruwenzorii vulcanius</i> Thomas, 1909		Mi- Ni	1
<i>Funisciurus carruthersi birungensis</i> Gyldenstolpe, 1927		Mi,Ki	1
<i>Tamsicus vulcanorum vulcanorum</i> Thomas, 1918		Mi	1
<i>Graphiurus murinus vulcanicus</i> Lönnerberg & Gyldenstolpe 1925	3900	Ki	1
	2810	Mg	2
	2500–3000	Sa, Vi	3
<i>Delanymys brooksi</i> Hayman, 1962	2980	Mg-Mu	2
<i>Dendromus c.f. insignis kivu</i> Thomas, 1916	2980	Mu	1
		Mg-Mu	2
<i>Lophuromys aquilus laticeps</i> Thomas & Wroughton, 1907	up to 4000	B,Ka, Ki,LC,	1
		LM, L,Mi,	
	2810, 2980	Mu,Ng, Sa,Mg,	2
	2400–3700	Mg-Mu	3
		Vi, Sa	
<i>Lophuromys woosnami</i> Thomas, 1906	2810, 2980	L, Mi, Ki, Mu,	1
	2400–3600	Sa,Mg, Mg-Mu	2
		Vi, Sa	3
<i>Arvicanthis abyssinicus rubescens</i> Wroughton, 1909		LC	1
<i>Dasymys incommis medius</i> Thomas, 1906	up to 2600	B, L, Sa,Ta	1
<i>Dasymys c.f. rwandae</i>	2810, 2980	Mg, Mg-Mu	2
<i>Grammomys c.f. dolichurus</i>	2810	Mg	2
<i>Hylomyscus aeta weileri</i> Lönnerberg & Gyldenstolpe, 1925	2400	Mi	1
<i>Hylomyscus vulcanorum</i> Lönnerberg & Gyldenstolpe, 1925	3700–3800	Ki, Mi	1
	2810, 2980	Mg, Mg-Mu	2
	2400–3400	Vi,Sa	3
<i>Lemniscomys striatus cf. massaicus</i> (Pagenstecher, 1885)		L	1
<i>Mus bufo bufo</i> Thomas, 1906	2700	B, Sa	1
	2810	Mg	2
	2540, 2850	Sa, Vi	3
<i>Mus gratus gratus</i> Thomas & Wroughton, 1910		Ni	1
<i>Mus triton birungensis</i> Lönnerberg & Gyldenstolpe, 1925	3400	Mi	1
	2980	Mg-Mu	2
<i>Oenomys hypoxanthus</i> (Pucheran, 1855)			1
	2810, 2980	Mg, Mg-Mu	2
	2820	Vi	3
<i>Praomys degraaffi</i> Van der Straeten & Kerbis Peterhans, 1999	2810	Mg	2
	3220	Vi	3
<i>Praomys jacksoni montis</i> Thomas & Wroughton, 1910		Sa,Ki,LM	1
<i>Thamnomys kempfi</i> Dollman, 1911	3900	Ki	1
	2810, 2980	Mg, Mg-Mu	2
<i>Otomys denti kempfi</i> Dollman, 1915	2800–3400	B,Mu,Sa,Ki	1
	2810, 2980	Mg, Mg-Mu	2
<i>Otomys tropicalis vulcanicus</i> Lönnerberg & Gyldenstolpe, 1925	2980	Sa	1
		Mg-Mu	2
<i>Tachyoryctes ruandae</i> Lönnerberg & Gyldenstolpe, 1925		L, LC,Mu	1
	2810	Mg	2
	2700	Vi	3

da side of the Virunga Volcanos (Mgahinga Gorilla National Park). Authors of taxon names of small mammals are included in Table 1 or may be found in Wilson & Reeder (2005).

Field methods

Both live and snap traps were used. The live traps were large Sherman folding traps (3"x3"x10"), and small, non-folding perforated traps (2"x 2 1/2"x 5 x 6- 1/2"). Both Live and Sherman traps were laid out in lines, 10 m apart (Tews et al. 2004), with five lines located randomly in each habitat at least 100 m away from human paths (Sutherland 2008). Snap traps were placed at the same points as live traps. Each trap was set for three nights. All traps were baited with crushed ground-nuts, meat and fish, bananas, and pieces of potatoes. They were checked daily between 0700h and 1000h and again between 1400h and 1600h. A locally made trap was used to collect mole rats (*Tachyoryctes ruandae*) in private cultivated plots adjacent to the park.

At each station, trapped animals were collected, processed and/or released (Nicolas & Colyn 2006). Live animals were placed in a zip-lock plastic bag and weighed using either 100 g or 500 g Pesola spring balances. A field identification was provided, sex determined and various measurements taken (head-body length, tail length, ear length, and hind foot length) using a ruler graduated in mm. Each newly captured animal to be released was marked by fur-clipping to ensure it could be recognized if subsequently recaptured.

Within each of the habitat types, the major plant species were recorded from the grids as follows: herbaceous zones used 2m² plots; shrub areas used 5m² plots; areas dominated by trees used 10m² plots. Plant species were identified from herbarium material at Karisoke Research Center (KRC) and from the Flora of Rwanda (Troupin 1977–1988). Temperature and wind speed were collected daily between 9:00–9:30 am, allowing comparison between different sites.

Data analysis

To standardize data for all habitats sampled so that species richness and diversity could be compared, trap success for each trapline (the number of animals caught per 100 trap nights) was calculated. The number of species trapped (per 100 trap nights) was also calculated for each site using the expression: [Species richness/Trap effort] x 100. The Shannon-Wiener (H) index of diversity was calculated for

all sites sampled and evenness values were derived from it.

$$H = - \sum (P_i * \ln P_i)$$

with H = the Shannon diversity index; P_i = fraction of the entire population made up of species i ; S = numbers of species encountered; and $\sum$ = sum from species 1 to species S . The Shannon index increases with the number of species in a community, and in theory, the Shannon index cannot exceed 5.0 (Krebs 1989). A high value of Shannon-Wiener index may indicate a large number for the species with similar abundances; a low value indicates lower species richness or domination by a few species. Evenness values (E) [$E = H / \ln (S)$] indicate how numbers of individuals are distributed among species in a community. When the evenness is high, the mammal fauna is more diverse and the species are equally abundant (Magurran 2005).

We tested non-parametric estimators available in EstimateS software (available at <http://viceroy.eeb.uconn.edu/estimates/EstimateS>) to estimate species richness as an alternative to the observed number of species in model Chao1. The classic richness estimators Chao1 was computed along with log-linear 95 % confidence intervals (Chao 2005, Colwell & Coddington 1994).

In order to estimate the number of additional species necessary to reach an asymptotic plateau, species accumulation rates were examined and were compared among each habitat type (Colwell et al. 2004). The calculation of species accumulation rates and the estimation of asymptotes/plateaux (species richness) were derived from the distribution of all individuals caught across habitats; species richness was estimated as a function of number of samples. If the curves became flatter with increasing effort (Chao 1 confidence bounds met or connected), it becomes less likely to detect new species in the additional samples.

Similarities of the small mammal communities in the different habitats were assessed using Bray-Curtis similarity indices and linked Cluster Analysis. Tukey's Honestly-Significant-Difference (Tukey HSD) tests were used for post-hoc comparisons when significant among-groups differences were indicated. To investigate the relationship between small mammal species and environmental factors, a Canonical Correspondence Analysis (CCA) was used. This is an indirect gradient analysis technique used to study the distribution of species along easily measured, recognizable environmental variables (Gauch & Whittaker 1972). The mole rat *Tachyoryctes ruandae* was found in cultivated fields outside the park, and it was not included in statistical analyses.

Table 2. Total numbers of individuals per species captured in the eight habitat types at VNP.

Species /Habitat/Altitude (m)	Mixed Forest	Swamp	Bamboo	Hagenia Woodland	Herbaceous	Brush Ridge	Sub Alpine	Alpine	Total
	2380–2580	2540	2540–2660	2740–3020	2900–3183	3220–3400	3420–3600	3640–3710	
<i>Crocidura tarella</i>					1				1
<i>Crocidura olivieri</i>	3			1	2	1		2	9
<i>Galerella sanguinea</i>						1			1
<i>Graphiurus murinus</i>	2	1		3					6
<i>Hylomyscus vulcanorum</i>	1	1	2	3	7	2	3		19
<i>Lophuromys aquilus</i>	8	15	4	8	24	15	15	10	99
<i>Lophuromys woosnami</i>	10	7	11	11	13	21	5		78
<i>Mus bufo</i>			1	1					2
<i>Oenomys hypoxanthus</i>				1					1
<i>Praomys degraaffi</i>						1			1
<i>Sylvisorex vulcanorum</i>				1					1
<i>Tachyoryctes ruandae</i>									(2)
TOTALS	24	24	18	29	47	41	23	12	218
Trap nights	300	300	300	300	300	300	300	300	2400
Density (Trap success %)	8.0	8.0	6.0	9.7	15.7	13.7	7.7	4.0	9.1
# species	5	4	4	8	5	6	3	2	12

RESULTS

Species richness

Small mammal trapping resulted in the capture of 220 individuals (208 rodents, 11 shrews, and one mongoose). Ninety-nine individuals were female while 121 were male. A total of eight rodent species, three shrews and one mongoose species were recorded. All rodents caught belonged to the subfamilies Murinae, Deomyinae, Rhizomyinae and Graphiurinae (Wilson & Reeder 2005). The most common species were *Lophuromys aquilus* (n=99) and *Lophuromys woosnami* (n=78), combining for 80.54 % of the individuals captured. These species were encountered in all habitats; all other species were rare (≤ 19.46 % of individuals captured in all habitats).

Small mammal species diversity was highest in *Hagenia* Woodland (8), intermediate in Brush Ridge (6), Herbaceous and Mixed Forest (5), Swamp and Bamboo (4) and lowest in Sub Alpine (3) and Alpine (2). Rodent captures were always more numerous than shrew captures (Table 2).

For Sub Alpine and Alpine zone Chao1 species richness estimator upper bounds reached horizontal plateaux (asymptotes), and its upper bound reached the lower bound for the bamboo and mixed forest (Fig. 2), so sampling effort can be considered adequate to reflect actual species richness. In other habitats, plateaux were not attained. Furthermore, species accumulation rates for habitat types and altitudinal range showed that the most species rich habitats in VNP were mid elevation habitats: *Hagenia* Woodland followed by Brush Ridge and Herbaceous.

Species diversity between habitats

A Bray-Curtis dendrogram based on all individuals captured showed that two species captured in Alpine represented distinct communities than those from other habitats. The Alpine (highest elevation at over 3600 m) and Bamboo habitats (lowest elevations of 2540–2660 m) had the least similar mammal communities (26.66 %) and species richness was low in both zones.

The effective number of species (Shannon diversity) was highest ($H > 1.0$) in *Hagenia* Woodlands and Brush Ridge, intermediate ($0.8 > H < 0.6$) in Herbaceous, Mixed Forest, Bamboo and Swamp and lowest in the Sub Alpine ($H = 0.2$) and Alpine habitats ($H = 0.1$). These differences in diversity indices were significant (Kruskal-Wallis test: $H_{7,40} = 20.49$; $p = 0.005$). The variation in community species (Evenness) also differed significantly among habitats types (Kruskal-Wallis test: $H_{7,40} = 20.49$; $p = 0.005$). The variation in community species were generally low (< 0.5), indicating that communities in all habitats were dominated by two species (*Lophuromys aquilus* and *Lophuromys woosnami*). Species diversity was negatively correlated with altitude. Altitude accounted for 20 % of the variation in species diversity with increasing altitude ($p = 0.004$).

Environmental correlates of community structures

The CCA-biplot (the first two axes) for environmental variables, habitat and small mammal abundances ex-

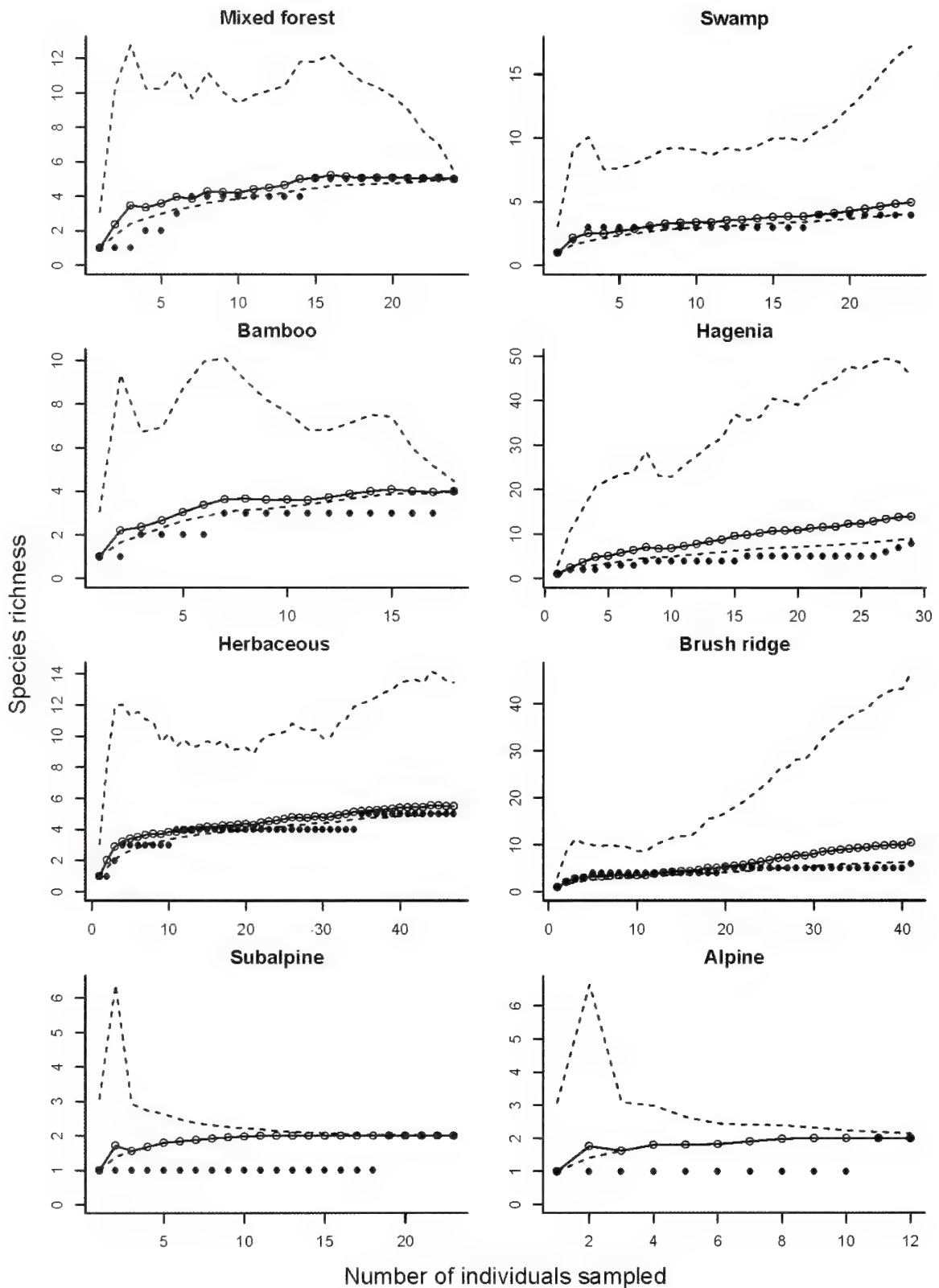


Fig. 2. Accumulation rates of observed and estimated (Chao1) richness. The black dots are observed number of species, the round circle represented Chao1 estimate, while dotted line is 95% confidence interval.

plained 19.3+39.4 (equals to 58.7 %) of variance in the data set (Fig. 3). The environmental variables that affected separation of sites and species along axis 1 most strongly were temperature, altitude, canopy cover, herbaceous cover and wind speed.

Lophuromys aquilus, *Lophuromys woosnami* and *Hylomyscus vulcanorum* plotted near the intersection of the axes, suggesting that these species are not strongly influenced by any of the six environmental variables and that they are habitat generalists. Furthermore, *Crocidura oliveri* kivu also seemed to be a generalist, and occurred in five habitat types. The percentage of canopy cover has a greater influence on the distribution of *Graphiurus murinus vulcanicus*, a primarily arboreal species.

DISCUSSION

Our study found few small mammal species at VNP compared to previous studies. The contiguous forest at Mgahinga National Park has 16 known rodent species and seven shrew species (Kerbis Peterhans & Austin 1996), eight of which were recorded during this study: *Hylomyscus vulcanorum*; *Lophuromys aquilus*; *Lophuromys woosnami*; *Oenomys hypoxanthus*; *Sylvisorex vulcanorum*; *Crocidura oliveri*; *Graphiurus murinus* and *Mus bufo*. Differences in size of the protected areas, trapping techniques, time of year, elevation, and habitats sampled may account for differences in species diversity with this adjacent site. The differences between sizes of sampled

areas and trapping methods might have influenced differences. For instance squirrels can be obtained using shotguns. Shrews are more easily captured with pitfalls. Gyldenstolpe (1928) covered the whole Volcanoes National Park, while this study has focussed on Mt Bisoke and the foot of Mt Sabyinyo.

Our study confirms a pattern of variation in species richness of small mammal communities along an altitudinal gradient. Habitat heterogeneity and altitudinal variations are a major factor affecting small mammal diversity (Isabirye-Basuta & Kasenene 1987; Stanley & Hutterer 2007). Mid elevation peaks in species diversity are common in both rodents and shrews whereas increasing elevation leads to fewer species. *Lophuromys aquilus* and *Lophuromys woosnami* are adaptable to the VNP habitats because they require moist scrub, forest, grassy, and tropical moist montane areas (Kingdon 1984). The elevational diversity might be related to climatic impacted factors such as rainfall, temperature, productivity, competition, resource abundance, habitat complexity, or habitat diversity (Lomolino 2001).

Species accumulation curves show insufficient sampling effort in six of eight studied habitats. Further, extreme weather during our sampling periods may have reduced trapping success. Some species previously collected in VNP were not captured during this study including *Crocidura niobe*, *Suncus megalura*, *Sylvisorex lunaris ruandae*, *Paracrocidura maxima*, *Myosorex babaulti* and eleven mice/rat species including *Delanymys brooksi*, *Dendromus insignis kivu*, *Dasymys incomptus*, *Dasymys*

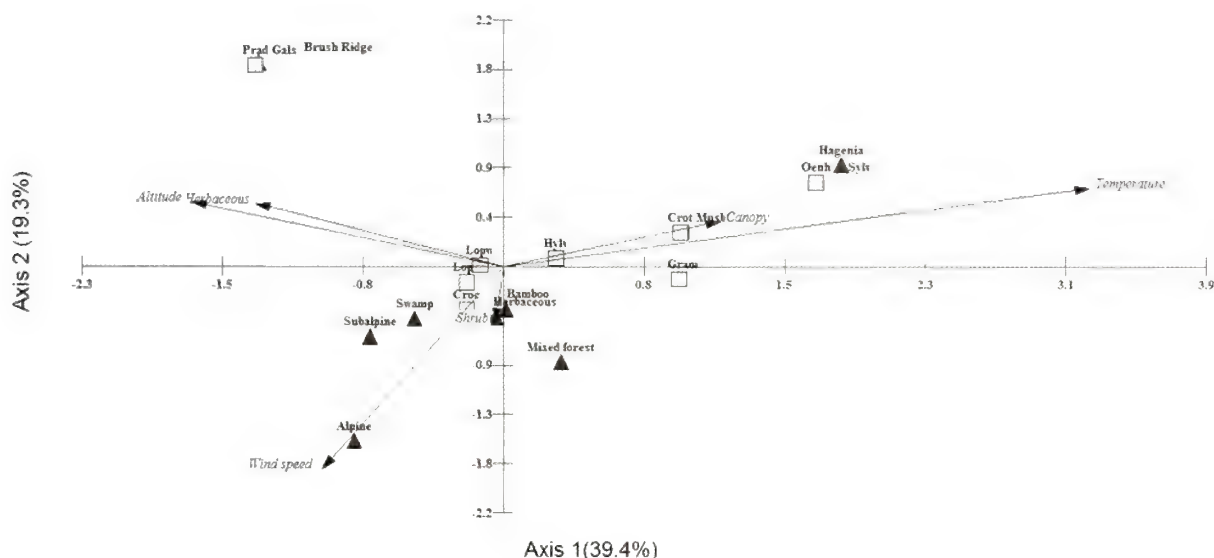


Fig. 3. CCA-biplot showing the influence of various environmental variables on small mammal distributions during this study period. Gram: *Graphiurus murinus*; Croc: *Crocidura tarrella*; Croc: *Crocidura oliveri*; Hylv: *Hylomyscus vulcanorum*; Lapq: *Lophuromys aquilus*; Lopw: *Lophuromys woosnami*; Musb: *Mus bufo*; Oenh: *Oenomys hypoxanthus*; Prad: *Praomys degraaffi*; Sylv: *Sylvisorex vulcanorum*; Gals: *Galerella sanguinea*.

c.f. *rwandae*, *Grammomys* c.f. *dolichurus*, *Hylomyscus aeta*, *Thamnomys kempfi*, *Otomys denti kempfi*, *Otomys tropicalis vulcanus*, *Mus triton*, *Mus gratus* (Gyldenstolpe 1928; Hutterer et al. 1987; Kerbis Peterhans & Austin 1996). More trapping over different seasons and with the added use of pitfall traps in more habitats are needed to adequately document small mammal communities at VNP.

The study area contains relatively few endemic species (six) compared with other Albertine Rift sites. This compares with twenty-one endemic species in the Ruwenzori Mountains of Uganda (Kerbis Peterhans et al. 1998), and 18 endemic species in Kahuzi-Biega forest (Kaleme et al. 2007). Five of the six endemic species and the one threatened species were found at low and middle altitudes at VNP.

Species from VNP have a high probability of survival owing to international and governmental protection efforts directed at the mountain gorilla (*Gorilla beringei beringei*), an 'umbrella species' from a conservation perspective. Since gorillas and endemic rodents and shrews depend on the same habitats, the conservation of the first acts to ensure the conservation of the second. In order to maximize the maintenance of biodiversity conservation in general and small mammals in particular, conservation efforts need to target both low elevation and mid elevation zones at VNP.

Our results have implications for how small mammal communities in VNP may alter with climate change. With increasing temperature, formerly low-elevation small mammal species may expand their ranges upwards while those of high-elevation species may contract, leading to changed community composition at mid- and high elevations (Moritz et al. 2008). More long-term monitoring is desirable to incorporate these factors, and to examine in detail how to mitigate these risks.

Our study indicates that the small mammal species have changed much since the pioneer study of Gyldenstolpe (1928). This may be a signal of concern for the conservation of this forest, and stresses the importance of regular small mammal surveys with close attention to associated habitats.

The problem of spatial scales is also important; 40 trap lines located at three study areas may not have been sufficient in a protected area of 150 km² and 40 km of width. Long-term studies are needed to better understand the effects of climatic events relative to those of local differences related to habitat structure. The findings of species accumulation rates and comparatively low richness during this study indicate that the small mammal species list for VNP is still incomplete and further inventory work is needed. We recommend that future, longer-term studies are carried out to confirm our species list, and to examine demographic processes and the impact of climatic changes on gorilla habitat.

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REFERENCES

- Chao A (2005) Species richness estimation. In: Balakrishnan N, Read CB, Vidakovic B (eds) Encyclopedia of Statistical Sciences. Wiley, New York: 7909–7916
- Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating and comparing incidence-based species accumulation curves. *Ecology* 85: 2717–2727
- Colwell R K, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society (Series B)* 345: 101–118
- Fischer E, Hinkel H (1992) Natur Ruandas: Einführung in die Flora und Fauna Ruandas. Ministerium des Inneren und für Sport Rheinland-Pfalz, Mainz
- Gauch HG & Whittaker RH (1972) Comparison of ordination techniques. *Ecology* 53: 868–875
- Golley FB, Ryskowski L, Sokur JT (1975) The role of small mammals in temperate forest, grassland and cultivated fields. In: Golley FB, Petrusiewicz K, Ryskowski L (eds) Small mammals: Their productivity and population dynamics. Cambridge University Press, Cambridge: 223–242
- Gyldenstolpe N (1928) Zoological results of the Swedish expeditions to Central Africa 1921. *Vertebra*. 5. Mammals from the Birunga Volcanoes, north of Lake Kivu. *Arkiv för Zoologi* 20A: 1–76
- Hutterer R, Van der Straeten E, Verheyen WN (1987) A checklist of the shrews of Rwanda and biogeographical considerations on African Soricidae. *Bonner Zoologische Beiträge* 38: 155–172
- Isabirye-Basuta G, Kasenene JM (1987) Small rodent populations in selectively felled and mature tracts of Kibale forest, Uganda. *Biotropica* 19: 260–266
- IUCN (2011) IUCN Red List of Threatened Species, version 2011, www.iucnredlist.org
- Kajonjoli S (1993) Inventaire systématique et répartition altitudinale des rongeurs dans un écosystème montagneux des volcans. Unpublished BSc thesis, National University of Rwanda, Butare
- Kaleme PK, Bates J, Kerbis Peterhans JC, Jacques MM, Ndara BR (2007) Small mammal diversity and habitat requirements in the Kahuzi-Biega National Park and surrounding areas, eastern Democratic Republic of Congo. *Integrative Zoology* 2: 239–246
- Kerbis Peterhans JC, Kityo RM, Stanley WT, Austin PK (1998) Small mammals along an elevational gradient in Rwenzori Mountains National Park, Uganda. In: Os-

- maston H, Tukahirwa J, Basalirwa C, Nyakaana H (eds) The Rwenzori Mountains National Park, Uganda. Exploration, environment & biology. Conservation, management and community relations. Makerere University, Kampala
- Kerbis Peterhans JC, Austin PK (1996) Small mammal component of the biological inventory of Kabiranyuma swamp, Mgahinga National Park, Uganda. Unpublished Report, Institute of Tropical Forest Conservation, Kampala
- Kingdon J (1984) East African mammals: An atlas of evolution in Africa. (Hares and Rodents). University of Chicago Press, Chicago
- Krebs JC (1989) Ecological methodology. Harper Collins, New York
- Lomolino VM (2001) Elevation gradients of species density: Historical and prospective views. *Global Ecology and Biogeography* 10: 3–13
- Magurran AE (2005) Ecological diversity and its measurement. Croom-Helm, London
- Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322: 261–264
- Nicolas V, Colyn M (2006) Relative efficiency of three types of small mammal traps in an African rainforest. *Belgian Journal of Zoology* 136: 107–111
- Owiunji I, Nkuutu D, Kujirakwinja D, Liengola I, Plumptre AJ, Nsanzurwimo A, Fawcett K, Gray M, McNeilage A (2005) The biodiversity of the Virunga Volcanoes. Technical Report (www.wcs.org/Albertine_Rift)
- Plumptre AJ (1991) Plant-herbivores dynamics in the Virungas. PhD thesis, University of Bristol, Bristol, England
- Robbins MM, Sicotte P, Stewart JK (2001) Mountain Gorillas: Three decades of research at Karisoke. Cambridge University Press, Cambridge
- Stanley, WT, Hutterer R (2007) Differences in abundance and species richness between shrews and rodents along an elevational gradient in the Udzungwa Mountains, Tanzania. *Acta Theriologica* 52: 261–275
- Sutherland WJ (2008) Ecological census techniques. Cambridge University Press, Cambridge
- Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31: 79–92
- Troupin G (1977–1988) Flore du Rwanda. Spermatophytes vols. I–IV. Musée Royal de l’Afrique Centrale, Tervuren
- Weber AW (1987) Ruhengeri and its resources: an environmental profile of the Ruhengeri Prefecture. ETMA/USAID, Kigali
- Wilson DE, Reeder DM (2005) Mammal species of the world: A taxonomic and geographic reference. Third edition. Johns Hopkins University Press, Baltimore